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Sex Change in the Hat Snail, *Calyptraea morbida* (Reeve) (Gastropoda: Calyptraeidae): An Analysis of Substratum, Size, and Reproductive Characteristics

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Abstract. The substratum, body size, and reproductive characteristics of the hat snail, *Calyptraea morbida,* from the west coast of Taiwan were studied. Among 416 snails attached to a substrate, 77.2% were found on the shells of *Turritella terebra,* which were usually occupied by the hermit crab, *Diogene spinifrons.* The shell margin of the female *C. morbida* was more irregular than that of the male. Moreover, *C. morbida* females on the shells of *T. terebra* were significantly heavier than those on smaller host shells (mostly *Turricula javana* and *Nassarius clathratus*). No such difference was found in males.

Female snails were significantly heavier than males. Individuals smaller than 18 mg were all male, whereas those larger than 202 mg were all female. Females had a shorter penis (< 2 mm) than that of the males (> 2 mm). A significant negative correlation between penis length and snail size was found in females but not in males. Brooding individuals were present almost year-round, with the highest occurrence in May. The recruitment of males (< 25 mg) occurred year-round, with a peak in July. Females smaller than 75 mg, on the other hand, were recruited between January and September, with the highest relative frequencies occurring in April. The size difference between sexes and reduction of penis length in females suggests that a life history involving sex change occurs in *C. morbida.*

INTRODUCTION

Sex change or sequential hermaphroditism is a phenomenon in which an organism functions first as one sex, then as another in the later stage. It is divided into three categories: protandry (males change to females), protogyny (females change to males), and alternating sexuality (repeated change of sex) (Warner, 1988; Wright, 1988; Heller, 1993). Protandry is widely scattered among invertebrates, while protogyny is very common among coral reef fishes (Policansky, 1982). Alternating sexuality might be rare in animals and it can be found in few species of bivalves and polychaetes (Coe, 1932; Policansky, 1982; Berglund, 1986; Heller, 1993; Premoli & Sella, 1995). Because sex change has evolved independently under many disparate circumstances, life history theory has sought to determine the conditions under which sex change is favored over either simultaneous hermaphroditism or gonochorism. A common explanation of sex change is the size (or age) advantage hypothesis, which predicts that sex change is favored when the reproductive success of the two sexes is different with respect to size (or age). For example, protandry may be favored when female egg production increases with size, while the ability of males to fertilize eggs is independent of size (Ghiselin, 1969; Warner, 1975; Charnov, 1982; Warner, 1988; Charnov & Bull, 1989; Collin, 1995).

Protandry has been documented in several groups of marine mollusks, including the gastropod superfamilies Calyptracea and Patellacea, and the bivalve superfamily Galeommatacea (Hoagland, 1978; Policansky, 1982; Heller, 1993). Among these, the gastropod family Calyptraeidae is the best known (Hoagland, 1978; Wright, 1988).

All species in the calyptraeid genus *Crepidula* Lamarck, 1799, which have been investigated to date are protandric (Coe, 1938; Hoagland, 1978; Heller, 1993; Warner et al., 1996). They attach themselves to hard substrata and are sedentary. Some species form large stacks consisting of large females, intersexed individuals, and small males [e.g., *Crepidula fornicata* (Linnaeus, 1758), and *Cr. onyx* Sowerby, 1824], while others form male-female pairs (e.g., *Cr. convexa* Say, 1822, *Cr. plana* Say, 1822). The timing of sex change might be influenced by the gender of conspecific neighbors (e.g., *Cr. fornicata* and *Cr. onyx*) (Coe, 1938; Hoagland, 1978; Warner et al., 1996). In contrast to *Crepidula,* sex change has been studied only in one species in the genus *Calyptraea.*

The sex change of *Calyptraea chinensis* (Linnaeus, 1758) differs from that of *Crepidula* in several aspects. In *C. chinensis* sex change always occurs at a certain age in its life history (Pellegrini, 1949; Wyatt, 1961) and not

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Table 1

Calyptraea morbida. Sizes of males and females in each collection. Numbers in parentheses indicate sample sizes.

Year	Month	Body weight[1] (mg)		Male only range	Overlapping range (m, f)	Female only range	Sex ratio[2] (male/all)
		Male	Female				
1991	April	40 (261)	140 (242)	4–34 (114)	35–200 (147, 189)	208–735 (53)	0.52^{ns}
	May	15 (15)	170 (7)	8–47 (14)	48–48 (1, 1)	52–223 (6)	0.68^{ns}
	July	27 (178)	160 (53)	1–44 (128)	45–140 (50, 19)	150–518 (34)	0.77**
	August	42 (133)	146 (62)	6–58 (91)	59–136 (42, 23)	138–596 (39)	0.68**
	November	26 (5)	110.5 (8)	8–55 (5)	no	60–295 (8)	0.38^{ns}
	December	48.5 (32)	166 (18)	10–79 (29)	80–113 (3, 3)	115–490 (15)	0.64*
1992	January	39 (176)	129.5 (32)	7–46 (111)	47–148 (65, 20)	160–347 (12)	0.85**
	March	61.5 (144)	177 (52)	8–57 (60)	58–162 (84, 23)	165–342 (29)	0.73**
	May	32 (656)	134 (327)	1–17 (126)	18–194 (530, 262)	195–388 (65)	0.67**
	September	63 (45)	177 (17)	9–41 (15)	43–146 (30, 5)	148–324 (12)	0.73**
	November	74 (27)	204 (15)	4–95 (18)	102–202 (9, 7)	204–468 (8)	0.64^{ns}
	Combined	37.5 (1672)	142 (833)	1–17 (248)	18–202 (2068)	203–738 (189)	0.66**

[1] Median of body weight. All comparisons of body weight between males and females were significant ($P < 0.01$, Mann-Whitney U-test).

[2] χ^2-test for sex ratios deviating from 1:1. ns: $P > 0.05$; *: $P < 0.05$; **: $P < 0.01$. If a sequential Bonferroni technique for correction of multiple tests (Lessios, 1992) is applied, seven tests, except the one from December 1991, remain significantly biased from 1:1.

at different times in different animals, as in *Crepidula*. *Calyptraea chinensis* breeds between December and May in Naples, Italy, with male recruitment occurring thereafter; and sex change occurs from January to March (Pellegrini, 1949; Bacci, 1951). Males and females are associated only during the breeding season when the smaller males are carried by the females. There appears to be no self-fertilization (Wyatt, 1960).

The hat snail, *Calyptraea morbida* (Reeve, 1859), has a limpetlike shell with a septum. It is distributed at depths

Table 2

Occurrences of *Calyptraea morbida* on different substrata from west coast of Chadin, Taiwan.

Substratum	Host shell			Total (%)
	Live	Empty	Occupied by a hermit crab*	
Gastropoda				
Babylonia formosae (Sowerby, 1866)	1	0	14	15 (3.6)
Ficus ficus (Linnaeus, 1758)	0	0	3	3 (0.7)
Nassarius clathratus	1	5	18	24 (5.8)
naticids	0	7	12	19 (4.6)
Turricula javana	1	8	20	29 (7.0)
Turritella terebra	0	78	243	321 (77.2)
Bivalves	0	5	0	5 (1.2)
Total (%)	3 (0.7)	103 (24.8)	310 (74.5)	416 (100.0)

* The hermit crab is *Diogene spinifrons*.

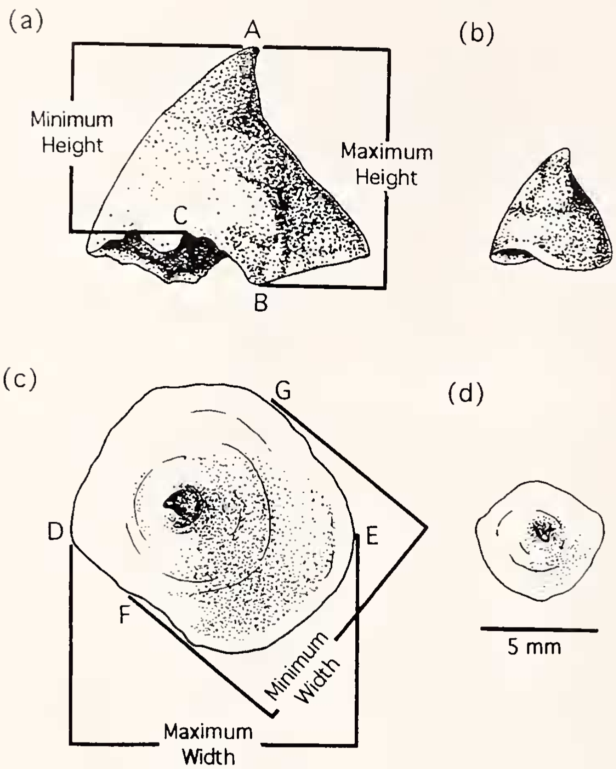

Figure 1

Calyptraea morbida. Shell morphology. (a) Left side view of a female shell, (b) Left side view of a male shell, (c) Apical view of a female shell, (d) Apical view of a male shell.

of 10–100 meters along the west coast of Taiwan and along the south-east coast of mainland China. It is found attached to mollusk shells housing hermit crabs and empty mollusk shells on the bottom of soft sediment. No published information on the life history of *C. morbida* is available. Therefore, it was previously unknown if these snails change sex. In order to elucidate the possible sex change of *C. morbida,* the present study examined the substratum, body size, and reproductive characteristics of the hat snail as well as its life history.

MATERIALS AND METHODS

Specimen Collection and Substratum Types

Specimens of *Calyptraea morbida* were collected by bottom dredging at 10–60 meters depth using a mesh size of about 1.1 cm along the west coast of Taiwan near Chadin (22°40′N, 120°09′E). A total of 11 collections were made between April 1991 and November 1992 (see Table 1). The specimens were kept in crushed ice during transportation; this practice may contribute to the high frequency of snails detached from their substate. If the snails were still attached to the substrate upon examination, both the snails and the substrate were kept in the same plastic bags. These specimens were fixed in 10% formalin and later preserved in 70% ethanol. The type of substrate (i.e., live mollusks, hermit crabs, and empty shells) was recorded for each hat snail. Since linear measurements of shells were not good indicators of size, the body weight without shell was used instead. After blotting with a piece of tissue paper, the wet body weight of each individual was measured on an electronic balance with a sensitivity of 1 mg. Some specimens in this study were deposited in the National Museum of Natural Sciences (serial# NMNS 002894) in Taichung, Taiwan.

Shell Morphology

The maximum and minimum height and width was measured for each shell (Figure 1) using a pair of vernier calipers for 90 specimens collected in April 1991. The ratio of minimum shell height to maximum shell height (RH) and the ratio of minimum shell width to maximum shell width (RW) were used to indicate the variability of the shell morphology which is mostly caused by substrate curvature and irregularities.

Size Structure and Reproductive Characteristics

All the specimens were sexed after dislodging the soft body from the shells. Females were distinguished by the presence of the white-colored capsule gland located on the right edge of the mantle, at the anterior of the columellar muscle. The presence of egg capsules containing

Table 3

Calyptraea morbida. Size comparison of snails on *Turritella terebra* and on other host shells.

Sex	Substratum	Body weight (mg) Median	Body weight (mg) Range	n	Mann-Whitney U-test
Male	*Turritella terebra*	45.5	1–180	178	$P > 0.05$
	Others*	39	10–202	59	
Female	*Turritella terebra*	179	18–596	143	$P < 0.01$
	Others	139	43–439	36	

* Including *Babylonia formosae, Ficus ficus, Nassarius clathrata,* naticids, *Turricula javana,* and bivalves.

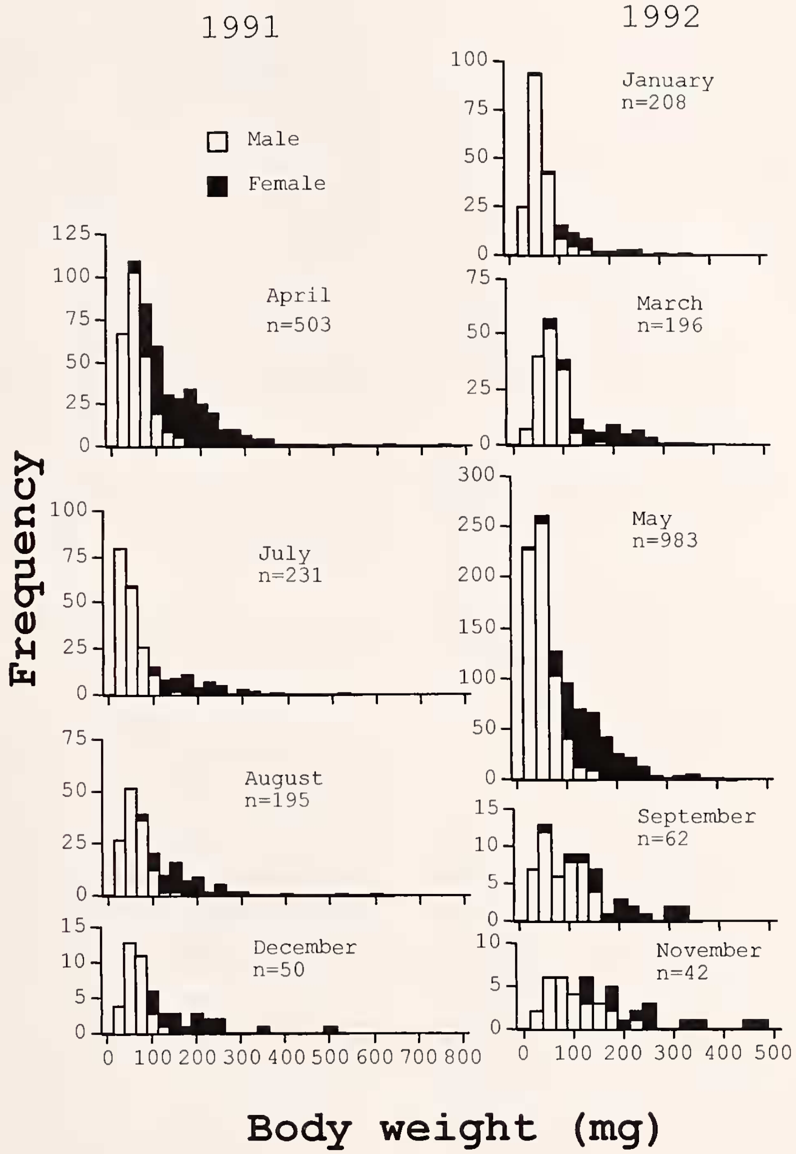

Figure 2

The size distributions of *Calyptraea morbida* in different months. The collections in May and November, 1991, with small sample sizes (n < 30), are not shown.

embryos could only be recorded for those females still attached to the substratum because in detaching females, the egg capsules were left attached to the substratum. Total numbers of embryos in all capsules were counted in 12 individuals to assess the relationship between snail size and fecundity. The lengths of penes were measured under a stereomicroscope for all specimens collected in April 1991.

A total of 31 hat snails (17 males and 14 females) were sectioned at 5 μm for histological gonad development study. Sections were stained with Harris hematoxylin and eosin.

RESULTS

Types of Substrata

Of 2505 specimens examined, 2089 individuals (83.4%) were found detached from their substrate, and 416 individuals (16.6%) were still attached to a substrate (Table 2). Among those attached, 77.2% occurred on the

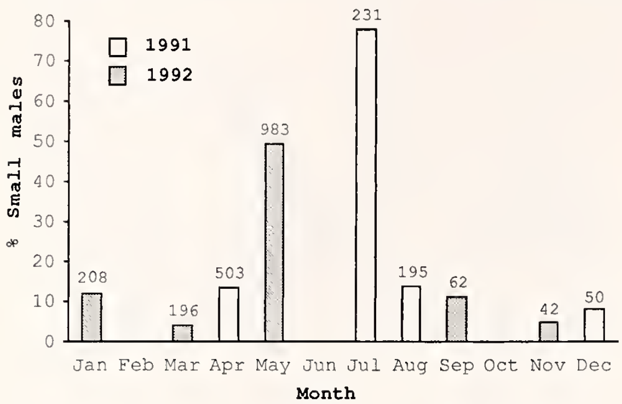

Figure 3

Calyptraea morbida. The annual change of the relative frequencies of small males (< 25 mg). Numbers above bars indicate sample sizes.

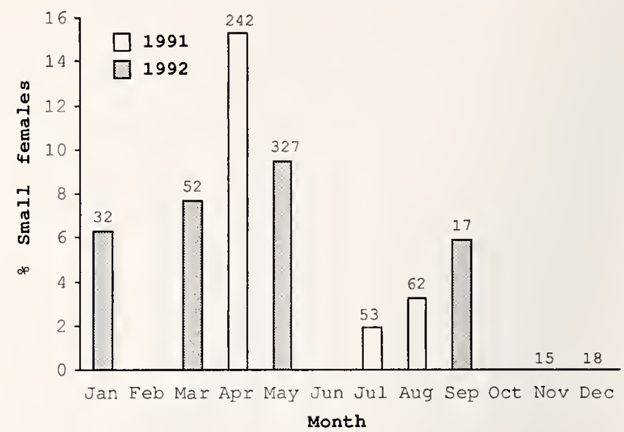

Figure 4

Calyptraea morbida. The annual change of the relative frequencies of small females (< 75 mg). Numbers above bars indicate sample sizes.

body whorl of shells *Turritella terebra* (Linnaeus, 1758). These host shells were mostly (74.5%) occupied by the hermit crab, *Diogene spinifrons*.

Shell Morphology and Size Structure

The shell of *Calyptraea morbida* is drawn as Figure 1. The shell margin of *C. morbida* was highly variable depending on the surface contour of the substratum. The RH and RW were used as indices to indicate shell variation. Seventeen out of 58 female shells and three out of 32 male shells had an RH value smaller than 0.76. Also, 15 out of 58 female shells and one out of 32 male shells had an RW value smaller than 0.80. In both of the above cases, the frequency of snails with extreme values of indices was dependent on the sex of the snails (Chi-square tests, $P = 0.03$ for RH, $P < 0.01$ for RW). Within the size range of 51–160 mg, in which individuals of both genders occur, females were found to have a significantly smaller RH (mean = 0.80, median = 0.79) than males (mean = 0.83, median = 0.83) (n = 58, $P < 0.05$ Mann-Whitney U-test). No such difference was found in RW. There is no significant correlation between RH or RW, and body weight in either males ($r^2 = 0.0004$ for RH, $r^2 = 0.0729$ for RW, $P > 0.05$) or females ($r^2 = 0.0036$ for RH, $r^2 = 0.0004$ for RW, $P > 0.05$). Thus the variation in shell morphology cannot be attributed to growth.

Since the shell margin was irregular, the relative size of the hat snail is expressed in term of the wet body weight. Females on the shells of *Turritella terebra* were significantly heavier than those on other substrata [mainly *Turricula javana* (Linnaeus, 1758) and *Nassarius clathratus* (Born, 1778)]. However, no such difference was found in males (Table 3). There was no size difference between the snails on empty shells and shells occupied by hermit crabs.

In this study a total of 2505 individuals ranged from 1 to 735 mg in wet weight. The size of females was significantly larger than that of the males in each of 11 samples ($P < 0.01$, Mann-Whitney U-test, Table 1). The size of males and females often overlapped, although in all collections the smallest animals were all males and the largest snails were all females (Table 1, Figure 2). After pooling all collections, the male-only range was 1–17 mg and the female-only range was 203–735 mg. The size range including both sexes was 18–202 mg, representing 25.2% of the total size range; and 82.6% of all individuals feel into this range. Males smaller than 25 mg, presumably recently recruited, were found in each collection throughout the study. The highest frequency of these recruiting males relative to all snails was found in July (Figure 3). Females smaller than 75 mg, presumed to have changed from males recently due to their sizes, were found between January

Table 4

Calyptraea morbida. The distribution of male and female snails on individual shells.

Group	Type	No. of observations	No. of snails
One-snail	Male	148	n = 277
	Female	129	
Two-snail	2 males	17	n = 118
	male-female	39	
	2 females	3	
Three-snail	2 males, 1 female	5	n = 21
	3 males	2	

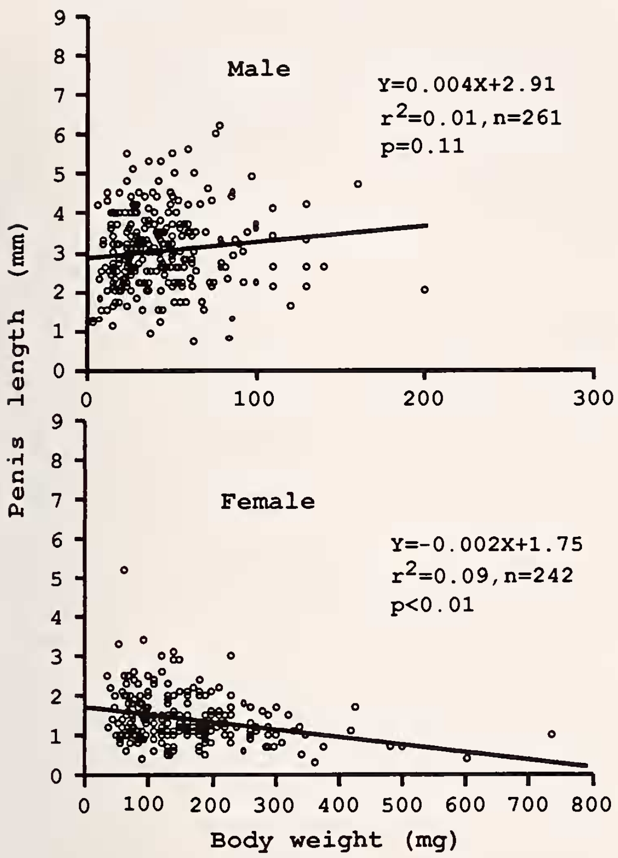

Figure 5

The relationship between *Calyptraea morbida* body weight and the length of penes for all snails collected in April 1991.

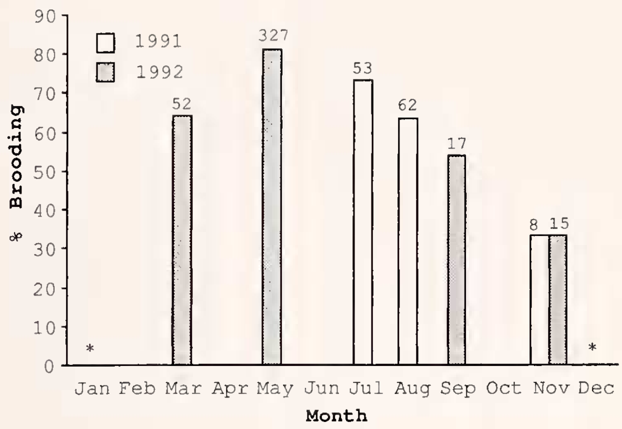

Figure 6

Calyptraea morbida. The annual change of the relative frequencies of brooding females. Numbers above bars indicate the total numbers of females that could be examined for the presence of egg capsules.
*Brooding individuals were found, but the frequency was not available in the month. No collection available in February, June, and October.

and September, with their highest frequency relative to all females appearing in April (Figure 4).

Reproductive Characteristics

Sex ratio: A total of 1672 males and 833 females were collected. The sex ratios of most (7/11) samples were significantly biased toward males, and none were female-biased (Table 1). Among those hat snails still attached to the substrata, most were solitary (66.6%) and the remainder were in groups of two or occasionally three (Table 4).

Histological examination and penis length: Among 17 males (range: 4–130 mg) examined histologically, the smallest male observed with sperm was 23 mg in wet body weight. Various stages of ovarian development were found in 14 sectioned females (range: 67–420 mg). None was seen with both sperm and oocytes together.

Most females (86.0%, n = 242) had their penes shorter than 2 mm, whereas the length of penis in most males (86.6%, n = 261) was longer than 2 mm. A significantly negative correlation between the length of penes and the size of snails was found in females but not in males (Figure 5).

Fecundity: The egg mass of an individual consists of a cluster of egg capsules each of which is connected by a filament to a sticky pad attached to the substratum. All embryos in a single brood were at the same stage of development. Females had brood at a variety of stages of development in every collection throughout the study period. The percentage of females with egg capsules was the highest in May (81%, Figure 6). Each female had 16–43 egg capsules per brood (n = 12, female size range 123–327 mg) and each capsule had 6–71 embryos. Release of planktonic larvae from the egg capsules was observed in the laboratory. Brooding females (median: 178 mg, range: 72–596 mg, n = 122) were significantly larger than non-brooding females (median: 150 mg, range: 18–468 mg, n = 57) ($P < 0.01$, Mann-Whitney U-test). The smallest brooding female was 72 mg. Large females were more likely to have egg capsules than small ones (Figure 7). Moreover, the fecundity increases with size ($r^2 = 0.40$, $P < 0.05$, n = 12) (Figure 8).

DISCUSSION

Type of Substrate

Calyptraeids often utilize shells occupied by hermit crabs as their substrata (Table 2) (Hendler & Franz, 1971; Hoagland, 1977a, b; Karlson & Cariolou, 1982; Shenk & Karlson, 1986; Vermeij, 1989). This association might increase the dispersal of males in calyptraeid species (Hen-

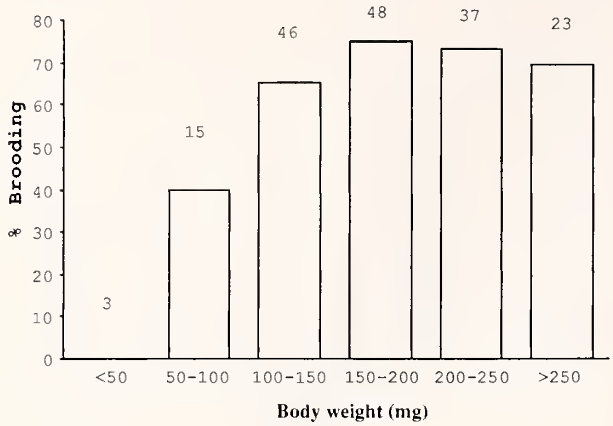

Figure 7

Calyptraea morbida. The percentage of females that are brooding in different size groups. Numbers indicate sample sizes. Data pooled from all collections.

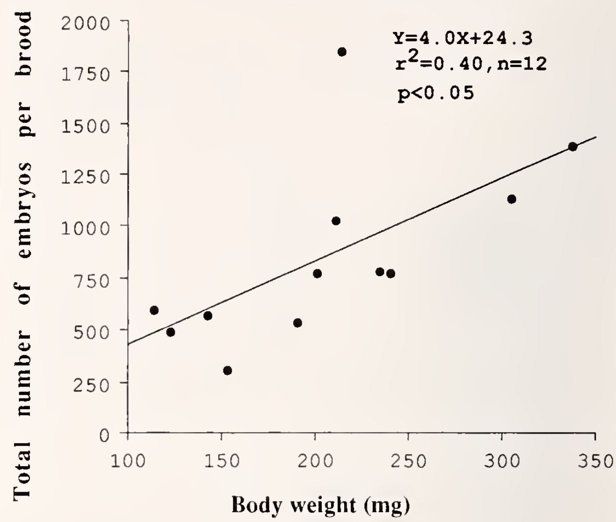

Figure 8

Calyptraea morbida. The relationship between total number of embryos and female body weight.

dler & Franz, 1971). On the other hand, the calyptraeids may feed on detritus stirred up and food particles dropped by the hermit crabs. If this feeding hypothesis is correct, the snails on hermit-crab-occupied-shells are expected to be larger than those on empty shells. No such difference was observed in this study (see Results).

Space available on the substratum might be an important limiting factor (Hendler & Franz, 1971). The sizes of *Calyptraea morbida* were different on various substratum types. This size difference might be explained by the fact that shells of *Turritella terebra* are larger than those of *Turricula javana* and *Nassarius clathrata.* The space limitation hypothesis is supported by the fact that substratum-related difference was found only in females which are larger than males (Table 3).

Shell Morphology

Shell morphology differs between males and females in shell margin curvature (Figure 1). The shell shape in the family Calyptraeidae is a variable character, strongly affected by the shape of the substratum (Hoagland, 1977a; Vermeij, 1989). It is likely that when a snail frequently changes its position, the extent of irregularity in shell margin will be less. Therefore, it is speculated that males, with high RH, might be moving more frequently than females. One might also suspect that the small size itself would render the RH of males higher than that of females. But for snails in the same size range, males were found to have higher RH than females (see Results). This result is compatible with the hypothesis that males may be more mobile than females.

Size Structure, Reproductive Characteristics and Sex Change

Females were larger than males in *Calyptraea morbida* (Table 1). This sexual dimorphism in size can be explained by differential mortalities, differential growth rates, or sex change (Wright & Lindberg, 1982). The following evidence in the present study is compatible with the hypothesis that individuals of *C. morbida* changed from male to female. First, the relative frequencies of females increased with size of *C. morbida* (Figure 2). All small snails (< 18 mg body weight) were males and all larger snails (> 202 mg body weight) were females throughout the year (Table 1). This pattern is compatible with the sex change hypothesis. Second, if this sexual dimorphism in size was caused by differential mortalities or growth rates, we expect to find some small recruited females. *Calyptraea morbida* recruits year round in Taiwan (Figures 2, 6). If sex change does not occur in its life history, small recruited females should be found throughout the year. However, all small snails were males in each sample (Table 1). This is incompatible with the differential mortality and the growth rate hypotheses. Third, penis length decreased with increasing size among females (Figure 5) and large females had only a vestigial penis. This phenomenon also occurs in other sex-changing snails in the Calyptraeidae (Fretter & Graham, 1962). Fourth, the overall sex ratio is biased toward males (Table 1) as expected in protandric species (Charnov & Bull, 1989). This phenomenon does not support the differential mortality hypothesis which predicts that the larger, long-lived females should outnumber males. All the above results strongly suggest that sex-change occurs in *C. morbida,* although no gonad of individuals was found with both sperm and oocytes together in the histological study (the same phenomenon also occurred in the protandric *Coralliophila violacea* [Chen et al., 1998]).

The size advantage hypothesis as it is applied to mollusks assumes that high female fecundity is related to large body size but high male reproductive success is related to mobility and therefore often to small size (Hoagland, 1978). In *Calyptraea morbida,* large females produce more embryos (Figure 8). The relationship between size and reproductive success in males, however, is not clear in this species.

Timing of Sex Change

The timing of sex change might depend on the size or age of the snails, or environmental factors such as food supply or the presence of conspecific neighbors. The following evidence in this study is more compatible with the hypothesis that *Calyptraea morbida* might change sex at a particular stage. First, if this snail changed sex at a certain size, the size overlap of two sexes should be narrow. However, the overlap in size of the two sexes spanned more than an order of magnitude (18–202 mg) (Table 1). Second, the "recruitment" of females, via male sex change, occurred almost year round, but was the highest in April (Figure 4). It is possible that males, with a peak recruitment between May and July (Figure 3), changed sex the next year after about 10 months of growth. In the congeneric *C. chinensis,* sex change occurs between the first and the second breeding periods when the males are 2–3 years old (Pellegrini, 1949; Bacci, 1951).

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